A Comparative Study of *Craspedacusta sowerbyi* and *Calpasoma Dactyloptera* Life Cycles[1]

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IN A PREVIOUS PUBLICATION (Matthews, 1963), immature medusae and mature hydranths of *Craspedacusta sowerbyi* were reported from aquaria of Mr. Mack Saki, a commercial guppy breeder of Honolulu. Whereas these medusae lived only three days, the hydranths persisted from October 1960 to November 1961 and, by hydranth and frustule budding, produced hundreds of hydranths, but no medusae.

Their reoccurrence on March 19, 1962 in aquaria of Mr. Saki (but not in mine) seemed again related to the water plant *Ceraptopterus thalictroides* (Matthews, 1963:20), but it harbored no hydranths. However, on internodes and leaf axils of *Elodea canadensis,* hydranths abounded. As before, immature medusae lived three days. The hydranths cultured in Petri dishes until December 1962 afforded material for continued study of factors reportedly responsible for medusa-bud formation.

Following Reisinger's (1934, 1957) methods, elevation of temperature from 20 C to 25–27 C failed to initiate medusa buds. Likewise, no maximal temperatures for hydranth, frustule, or medusa budding were found (McClary, 1959), nor were seemingly antagonistic budding stages altered either by feeding rates or temperature levels (Lytle, 1961). In short, cultures were cooled and warmed, starved and surfeited, isolated and crowded, coddled and coerced, without one medusa or tentacular hydranth resulting. As might be expected, no hydranths were living by December 30, 1962.[3]

Quite by chance, on 30 untreated "bunches"

of *E. canadensis* purchased March 3, 1963, atentacular and tentacular hydranths were observed. Although most atentacular hydranth stages of this study are from the Saki material, all tentacular hydranth stages are from this new source (March 3, 1963 to date).

For 18 months (March 1963 to August 1964) atentacular and tentacular hydranths have lived in my laboratory, either together in the same culture or isolated in separate cultures; and so striking is their resemblance that, although a tentacular hydranth stage of *C. sowerbyi* had not been mentioned previously (Browne, 1906; Crowell and Lytle, 1955; Dejar, 1934; Dunham, 1941; Fowler, 1890; Goette, 1909, 1920; Gaw and Kung, 1939; Hadzi, 1959; Kramp, 1950; Kuhl, 1947; Lytle, 1961; Matthews, 1963; McClary, 1959; Moser, 1930; Payne, 1924, 1926; Pennak, 1959; Potts, 1906; Reisinger, 1934; Romanes, 1881; Ryder, 1885; Uchida, 1955, 1963; and Woodhead, 1943), there seemed little doubt that this was but an aberrant form of a single, dimorphic species.

The purpose of this paper is threefold: (1) to verify Buchert's (1960) atentacular and tentacular stages, (2) to question, in light of my findings, the relationship he ascribes to certain of these stages, and (3) to report, for the first time in Hawaii, stages in the life cycle of *Calpasoma dactyloptera* (Fuhrmann, 1939).

IA. ATENTACULAR HYDRANTHS OF MIXED CULTURES

Small portions of *Elodea canadensis* with attached atentacular and tentacular hydranths were placed in Petri dishes containing 30 ml of aged tap water. Although some cultures were allowed to evaporate almost completely, most were maintained at the 30 ml level.

Temperatures varied from 20.5 C to 28.0 C, with the mean at 26.5 C. The pH ranged from

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[3] While I was searching for new material, both atentacular and tentacular hydranths were undoubtedly present all the time in aquaria on my own lanai, where subsequently they were found!

6.5 for new cultures to 8.5 for old, well-established cultures, with the mean at 7.5.

The number of hydranths per culture was restricted by removal of frustules of 10 atentacular and 10 tentacular hydranths.

Cultures remained covered except when hydranths were observed or when an oligochaete (*Aeolosoma hemprichi*) and turbellarians (*Planaria* sp. and *Stenostomum tenuicaudatum*) were introduced (Nuttycombe and Waters, 1938). These were directed by "minuten Nadeln" to make contact with a capitulum. Then, unlike small nematodes whose snake-like movements stopped as if the animal had been electrocuted (Matthews, 1963:20), *Planaria* continued to struggle even after its twisted, contorted body was completely ingested. Because a small worm usually filled a single hydranth's enteron, its constriction allowed the severed "posteriors" of large *Aeolosoma* and *Stenostomum* to gyrate blindly.

In colonies, unfed hydranths remained "hungry" even after ingested contents of fed hydranths cleared and presumably could have been freely shared. If clearing denoted digestion, it is interesting that it began just below the mouth and proceeded toward the attached basal portion. This was observed in a two-hydranth colony starved for three days and then fed *Planaria* whose pharyngeal region was gorged with carmen. Contact with one of the capitula was made at 7:50 AM. By 8:00 AM ingestion was complete and already the portion nearest the hydranth's mouth was beginning to clear. By 8:10 AM movement down the enteron had progressed halfway and, although the end nearest the hydranth's mouth was clear, the end farthest removed was only beginning to be so. By 8:30 AM the mass of carmen particles and the remains of the worm entered the base of the unfed hydranth, and by 10:00 AM had ascended one-third its column. The position of the mass as such did not further change. However, with digestion apparently completed, diffuse, minute red granules indicated that phagocytosis had also occurred.

This experiment was repeated the following day on the same colony. Once again ingestion required only 10 minutes and, as before, digestion seemed most pronounced in the region immediately below the hydranth's mouth. Again, in ½ hr the almost completely digested mass reached the base of the hydranth but, instead of entering the base of the other hydranth, it ascended the column just descended. And, although ascending the first half required almost 2 hr, ascending the last half, plus complete egestion, required only 10 minutes. As before, small red granules remained, indicating that some phagocytosis had taken place. Whether or not sharing occurred, the unfed hydranth instantly accepted a new worm whereas the fed hydranth repeatedly rejected it. This, however, may have been more the result of unspent nematocysts in the unfed hydranth and of spent nematocysts in the fed hydranth than the result of hunger per se.

Discussion pertaining to feeding tentacular hydranths is postponed until later.

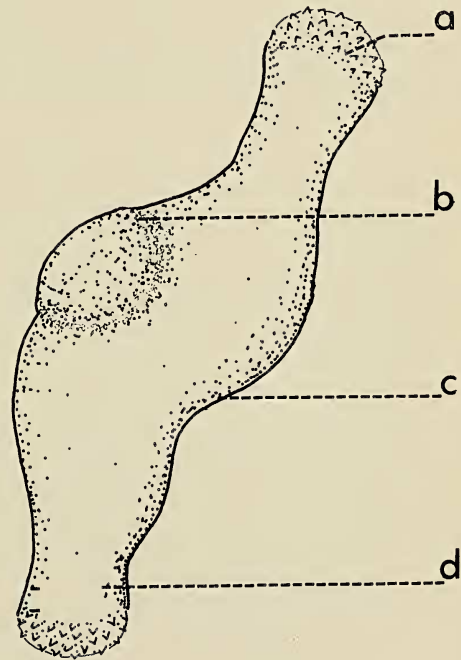Figures 1–4 are drawings of atentacular hydranths from which detritus and algae (*Tribo-*

FIG. 1. *Craspedacusta sowerbyi. a, d,* Two atentacular hydranths; *b,* developing bud; and *c,* centrally located attachment point.
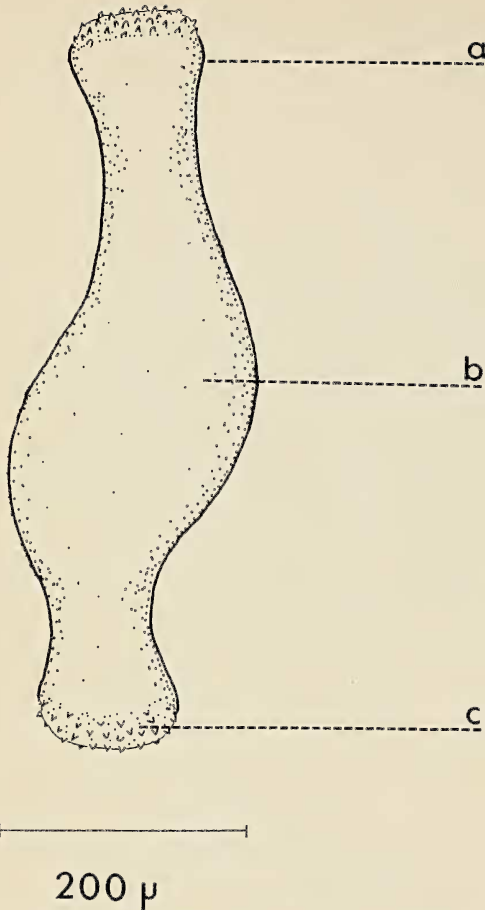
Figure 1 (*a, d*) and Figure 2 (*a, c*) are really not comparable with those of Figure 3 (*a, b, c, e*) or with those usually shown by other workers. As will be explained later, hydranth buds form as lateral outpocketings of existing hydranths, and thus size differences accompany age differences. Hydranths of Figure 1 (*a, d*) and Figure 2 (*a, c*) are of the same size and the same age. This will be explained subsequently under frustule development.

Figure 4 with its almost completely liberated frustule (*a*), its three hydranths (*b, c, e*), its attachment region (*d*), and Figure 5 with its two hydranths (*c, d*), its attachment region (*e*) on the node (*f*) of *E. canadensis* and its frustule (*b*) correspond well with those of Buchert's stages (Fig. 13, row III), although the actual site of frustule budding is different. Payne (1924:430, pl. 10, fig. 64) also indicates that frustule budding occurs in the lower rather than in the upper one-third of the hydranth's column. Although the probable purpose of their figures was more to record frustulation than to depict its actual site, nevertheless, the hypostome region with its higher metabolic rate (Burnett, 1961:427) is the one usually selected. Thus,
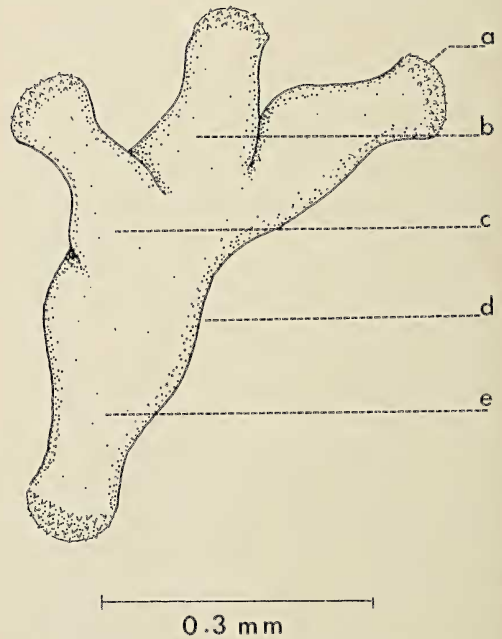

200 μ

FIG. 2. *Craspedacusta sowerbyi. a, c,* Atentacular hydranths developing from both ends of the frustule; and *b,* attachment.

nema bombycina and *Fremyella diplosiphon*) have been removed. In Figure 1 the two atentacular hydranths (*a, d*) and the centrally located attachment point (*c*) correspond well with Buchert's stages (Fig. 13, row I), except that my developing bud (*b*) ultimately became a hydranth whereas his became a medusa (*a*). However, one need only refer to Payne (1924: 430, pl. 10) for confirmation of Buchert's row I stages.

Figure 2 with its two hydranths (*a, c*), its basal attachment region (*b*), and Figure 3 with its four hydranths (*a, b, c, e*) and its basal attachment region (*d*) correspond well with Buchert's stages (Fig. 13, row II). It should be pointed out, however, that my hydranths in

0.3 mm

FIG. 3. *Craspedacusta sowerbyi. a, b, c, e,* Four atentacular hydranths; and *d,* attachment region.

Figures 6, 7, and 8 show tentacular hydranths either as they occur naturally on stems and leaves of *E. canadensis* or as they appear on the bottom of Petri dishes with detritus and algae (*T. bombycina* and *F. diplosiphon*) removed. Thus, Figure 6*B, C,* and *D* represent tentacular stages which once occupied positions on a leaf of *E. canadensis* similar to those of tentacular stage *A.* However, in old, neglected cultures a thick algal mat may cover the bottom of the Petri dish and in, and frequently below, this mat tentacular hydranths are observed which are extremely hyaline. Near the bases of these old hydranths sometimes one, but frequently many, small spherules develop (Fig. 6*B, C, D*). From these metamorphose, after perhaps a month or more of delay, small tentacular hydranths. By this time the parent hydranth may be completely consumed. Thus, with the possible exception of body shape these stages (Fig. 6*A, B, C, D*) correspond well with those of Buchert's stages (Fig. 14, row IV).

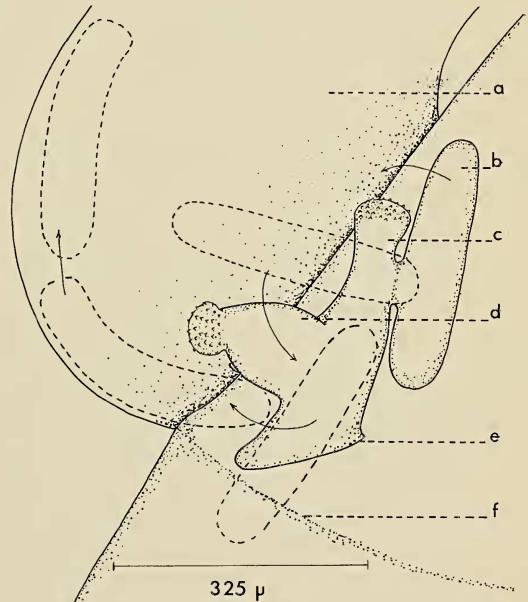Figure 7 represents frustule budding, a phenomenon frequently observed in young, vigor-

FIG. 4. *Craspedacusta sowerbyi. a,* Almost completely liberated frustule; *b, c, e,* three atentacular hydranths; and *d,* attachment region.

with the possible exception of frustule fragments and spherules, Buchert's stages (Fig. 13, rows I, II, III) add little that is new to our knowledge of *C. sowerbyi* atentacular hydranths.

IB. TENTACULAR HYDRANTHS OF MIXED CULTURES

As previously stated, small portions of *E. canadensis* placed in Petri dishes in 30 ml of aged tap water contained tentacular as well as atentacular hydranths. Thus, the conditions under which atentacular hydranths were observed apply equally to tentacular hydranths.

FIG. 5. *Craspedacusta sowerbyi. a,* A leaf portion of *Elodea canadensis; b,* budding frustule and its migration (*arrows and dotted outline*); *c, d,* two atentacular hydranths; *e,* attachment region; and *f,* nodal region of *E. canadensis* stem.
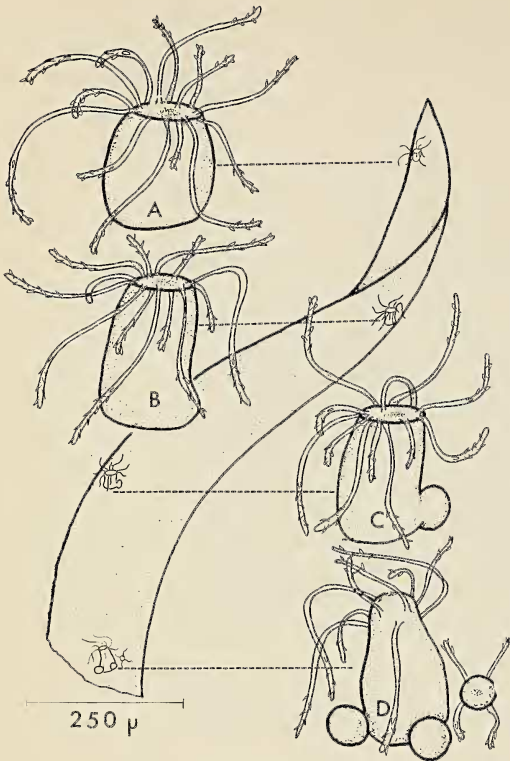
FIG. 6. Portion of *E. canadensis* leaf. *A*, Tentacular hydranth; *B* and *C*, tentacular hydranths forming spherules; and *D*, metamorphosis of a spherule into a small tentacular hydranth.
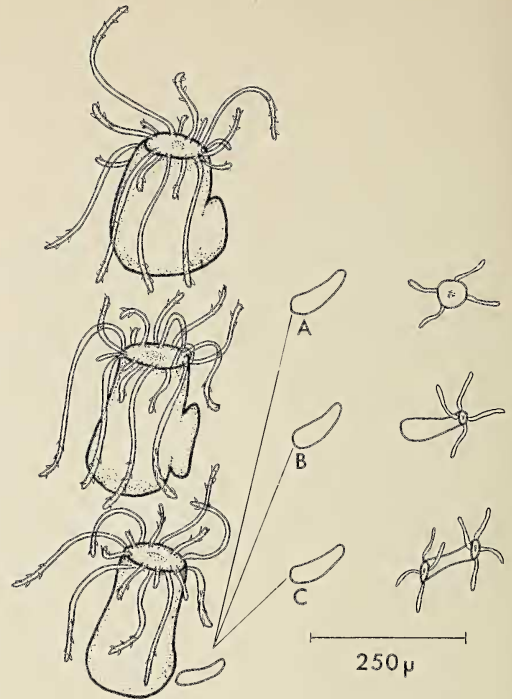

FIG. 7. Frustulation in a tentacular hydranth. *A*, Frustule forming a spherule with four tentacles; *B*, frustule forming a small tentacular hydranth; and *C*, frustule forming tentacles at both ends.

ous tentacular hydranths. This approximates frustule budding in atentacular hydranths, except that in tentacular hydranths the process may occur anywhere along the hydranth column, not necessarily near the hypostomal region. These small frustules may form spherules which develop tentacles (*A*); or may form tentacles directly at their thinner end (*B*); or may form tentacles simultaneously at both ends (*C*) even before the frustule attaches. Thus, from a frustule axle, tentacles may radiate like spokes from each end. Later, one end slowly rises from the bottom of the Petri dish and forms an asymmetrical V, i.e., one side is shorter than the other. Only when the complete metamorphosis from frustule to tentacular hydranth is observed can one say with certainty which is bud and which is parent. This, as previously stated, is quite different from true hydranth budding.

Again, except for slight differences in body shape, these stages (Fig. 7*A*, *B*, *C*) correspond well with those of Buchert's stages (Fig. 14, row V).

Figure 8 represents a piece of *E. canadensis* on which hydranth-budding tentacular hydranths (*A*, *B*, *C*, *D*) and atentacular hydranths are located; the latter, for the sake of clarity, are omitted although in leaf axils of this very portion atentacular hydranths occurred. This point is stressed, for it is important that we realize that both tentacular and atentacular hydranths can occur simultaneously under the same environmental conditions.

Figure 8*B* is of particular interest because, since atentacular hydranths had apparently lost their ability to form medusa-buds, this function, I reasoned, had been taken over by small frustules (Fig. 8*B*, *a*). Food brought to tentacles elicited little or no response, but this was expected, since readiness to forage should have been preceded by movements of tentacles and velum. I waited. Days passed. Impatient at the

rate of metamorphosis, I freed with dissecting needles a "medusa" like that indicated by *A* and brought it to the surface. It sank slowly without so much as a single twitch. Rather than medusae metamorphosing from small frustules (*B, a*) these were, in reality, tentacular hydranths whose buds (*B, a*) developed tentacles and remained attached (*C, b* and *D, c*).

Thus, stages in tentacular hydranth budding (Fig. 8*A, B, C, D*) are comparable to those figured by Buchert (Fig. 14, row VI). It is some consolation now to learn that Buchert, too, first thought these "were larval forms out of which the medusa develop" (Buchert, 1960: 34).

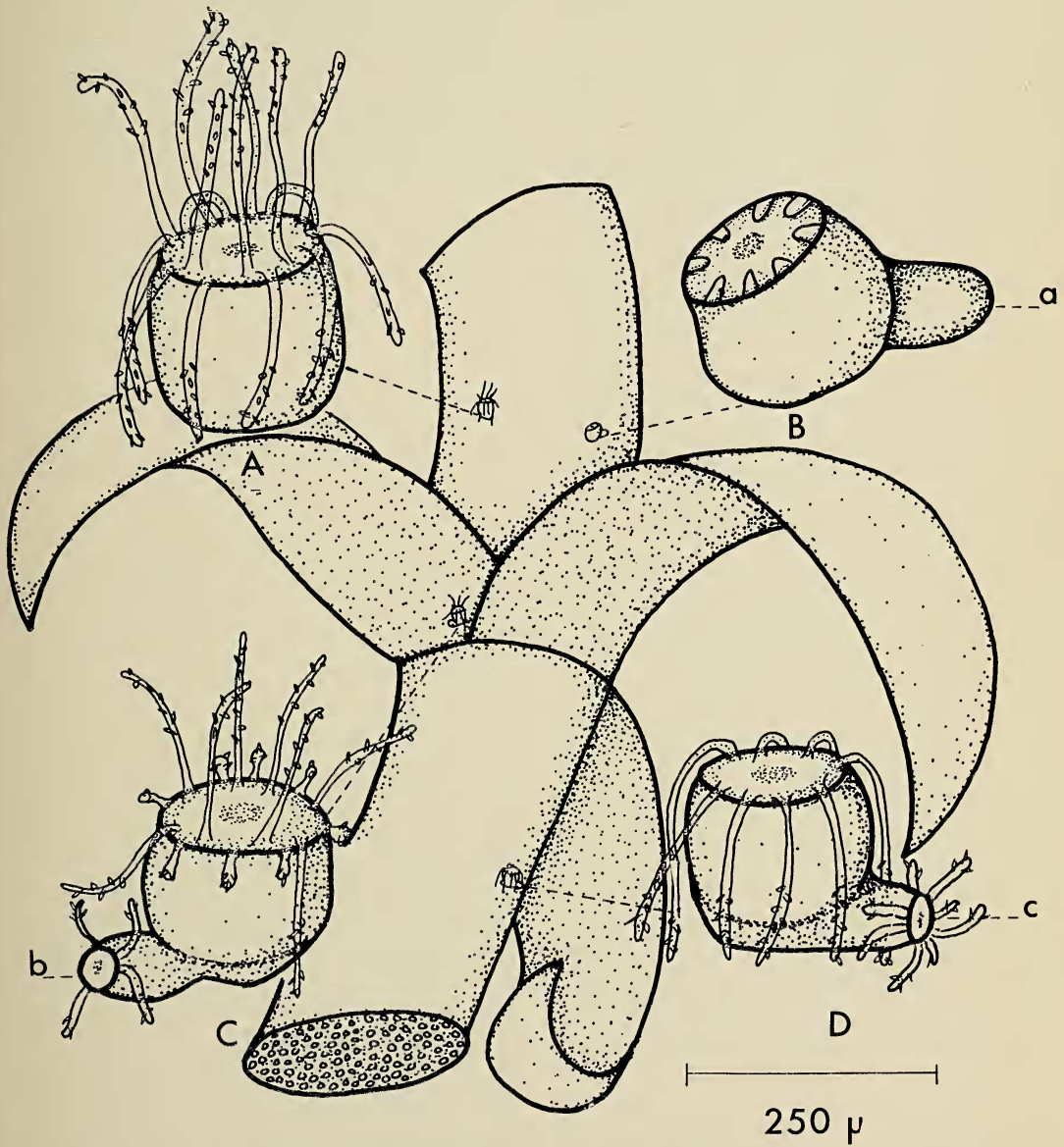Thus, all of Buchert's atentacular (type A)

FIG. 8. Portion of *E. canadensis. A,* Medusa-like, tentacular hydranth; *B,* small, medusa-like hydranth with contracted tentacles and young bud (*a*); *C,* tentacular hydranth and bud (*b*) with four tentacles; and *D,* tentacular hydranth and bud (*c*) with eight tentacles.

and tentacular (type B) stages are accounted for. Although this strengthens his one species concept, its proof rests in: (1) the ability to demonstrate conclusively that frustules (Fig. 13 A-B) or frustule fragments (C) of atentacular hydranths can metamorphose into tentacular hydranths (Fig. 14A), and (2) that tentacular hydranths (Fig. 14B) can metamorphose into atentacular hydranths (Fig. 13D). If this cannot be demonstrated, then two similar but different species must exist.

To prove or disprove this, a more detailed and accurate study of frustules was needed. Previously, these had been collected from mixed cultures; now they must be obtained from cultures rigorously isolated. Therefore, careful precautions were taken against contamination.

II. THE RELATIONSHIP BETWEEN CERTAIN ATENTACULAR AND TENTACULAR STAGES

A complete set of equipment was placed in each of separate but adjoining rooms in the laboratory. This consisted of Petri dishes, pipettes, dissecting needles, thermometers, etc. Each set remained in its respective room and was checked before each day's work. Each room had its own *Aeolosoma hemprichi* cultured on rice-agar plates following the method of Brandwein (1937), and its own supply of aged tap water and pond water filtered through millipore filters of 0.45 μ pore size.

Although they were not absolute safeguards against contamination of one culture with another, results proved these precautions adequate.

Frustules were collected and cultured from previously isolated cultures. The number of atentacular and tentacular cultures was restricted to 20 each, from which the following information was obtained: (1) type of culture; (2) length, width at thicker end, width at thinner end; (3) change in shape; (4) size of frustule divisions; (5) change in position (i.e., horizontal to vertical); (6) change in location (i.e., locomotion; and (7) date of capitulum or tentacle formation.

Previously, measurements in microns of the first frustule observed in each of 20 mixed cultures showed these variations: lengths 575–75, mean 375; widths, thicker end 125–37, mean

87; widths, thinner end 75–37, mean 54.

Figure 9A shows this frustule drawn to the same scale as other frustules. Measurements in microns of frustules from isolated atentacular hydranths (before any division of these frustules occurred) showed these variations: lengths 575–375, mean 465; widths, thicker end 125–100, mean 106; widths, thinner end 100–75, mean 83. Figure 9B shows the size of this frustule drawn to the same scale.

Although division was observed in frustules measuring 575–425 μ, no division was observed in frustules measuring 375 μ. The following five examples are typical of frustule lengths and the lengths of pieces into which they divided:

LENGTH OF FRUSTULE (μ)	LENGTH OF PIECES (μ)	
	Short	Long
575	150	425
500	175	325
425	175	250
400	150	250
400	150	250

The short pieces showed these variations (measurements in microns): lengths 175–150, mean 160; widths, thicker end 75–55, mean 65; widths, thinner end 50–37, mean 42. Figure 9C shows the size of the small frustule fragment drawn to the same scale.

The large pieces showed these variations (measurements in microns): lengths 425–250, mean 300; widths, thicker end 100–75, mean 82; widths, thinner end 75–37, mean 54. Figure 9D shows the size of the large frustule fragment compared to sizes of other frustules.

Buchert (1960:47) lists the following variations for his Type A (atentacular) frustules (measurements in microns): lengths 635–441, mean 475; widths, thicker end 134–96, mean 118; widths, thinner end 96–76, mean 88. Figure 9E shows the size of this frustule compared with sizes of other frustules. Although these data do not lend themselves to statistical analyses, they do suggest some interesting possibilities.

Frustule A is smaller than frustule B because

mixed cultures would contain fragments of atentacular frustules and (as will be shown directly) small frustules of tentacular hydranths. In isolated cultures of atentacular hydranths, where frustules are allowed to divide before samples are taken, Figure 9B would approximate A. Since my selected B frustule so nearly approximates Buchert's E, one might assume that Figure 9E frustules were also selected before any of them divided (Fig. 13A–C).

Measurements in microns of the first frustules observed in each of 20 isolated, tentacular cultures showed these variations: lengths 225–75, mean 150; widths, thicker end 75–50, mean 55; widths, thinner end 50–37, mean 45. Figure 9F shows the size of this frustule compared with
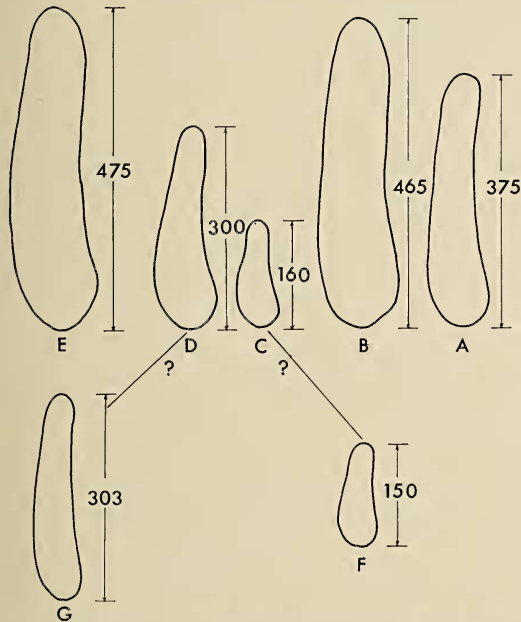

FIG. 9. Schematized frustules drawn to the same scale. A, Mean length and widths (thicker end, thinner end) of the first frustule observed in each of 20 mixed cultures; B, mean length and widths of first frustules observed from isolated atentacular hydranths before any division of frustules occurred; C, small fragment of a frustule; D, large fragment of a frustule; E, Buchert's atentacular frustule; F, tentacular frustule; and G, Buchert's tentacular frustule. (*Question marks* suggest possible relationships between C–F and D–G.) All measurements are in microns.

sizes of other frustules. Buchert (1960:47) lists the following variations for his Type B (tentacular) frustules (measurements in microns):

lengths 442–172, mean 303; widths, thicker end 78–48, mean 62; widths, thinner end 58–38, mean 48. Figure 9G shows the size of this frustule compared with sizes of other frustules.

Even without the application of statistical analyses the similarity of small fragment Figure 9C with frustule Figure 9F is striking, and suggests quite convincingly how one might be mistaken for the other. This is undoubtedly what I had done. I have no explanation why Figure 9G (Buchert's tentacular frustule) more nearly approximates Figure 9D (except for thicker width of D) than it does Figure 9F.

This much is now known: In isolated atentacular cultures, not only do large frustules (Fig. 9B) metamorphose directly into atentacular hydranths, but, more important, so do their fragments (Fig. 9D, C). Furthermore, in isolated tentacular cultures frustules metamorphose only into tentacular hydranths.

Change in frustule shape is considered here for two reasons: (1) its relation, if any, to frustule fragmentation, and (2) its relation to locomotion. Frustules of both atentacular and tentacular hydranths exhibit peculiar waves of contractility which slowly pass from one end of the frustule to the other. Figure 10 is a diagrammatic representation of these waves as observed in a 525-μ frustule of an atentacular hydranth. (In the figure, numbers correspond to ocular micrometer spaces of 25.) When first observed (Fig. 10A), this frustule appeared as if about to divide into a fragment 150 μ long, and a fragment 375 μ long; however, 15 minutes later the region of contractility had moved 100 μ (Fig. 10B). In another 5 minutes the region of contractility had moved an additional 75 μ (C); 5 minutes later another 75 μ brought the area of contractility to within 125 μ of the wider end (D). Then, 9 minutes later, the wave of contractility had completely traversed the frustule (E)—in the observed elapsed time of 34 minutes. If one adds another 10 minutes for the wave to reach the point where first observed (A), 45 minutes would be a conservative estimate of the time required for a wave to traverse the entire length of the frustule. Rarely, however, is frustule change of shape so simple. Figure 10F, G, and H clearly show that more than one wave may be operative and, although

these were not accurately timed, their rates appeared to be synchronized. This is much slower than the rate of contractility recorded for *C. sowerbyi* frustules by other workers (Crowell and Lytle, 1955:255). Furthermore, although this process may have something to do with locomotion, the contractile waves associated with Figure 10*D, E, F, G* and *H* are those of a frustule already attached. While certain of these contractile waves (Fig. 10*E, F, G, H*) might serve to carry developing nematocysts into the forming capitulum, other waves seem to carry materials in the opposite direction; thus their function remains obscure. Fifteen hours later the once horizontal frustule had assumed a vertical position and already a capitulum was formed. No divisions occurred.

On October 23, 1963, five atentacular colonies were placed in approximately 20 m/c of Zn[65] diluted with 30 ml of filtered culture water. The purpose of this experiment was to follow "hot" frustules through several generations in an attempt to prove that, in mixed cultures, only atentacular hydranths would be radioactive. A reciprocal experiment was planned for the frustules of tentacular hydranths. These experiments

are being repeated, using a Packard Tri-carb liquid scintillation counter and weak (low energy) Betas in the hope that the possibility of knocking out tentacle-forming mechanisms might be lessened.

Figure 11 shows frustule budding and locomotion which occurred on October 30, 1963 in three of five radioactive, atentacular hydranths. This is included not because it is normal but, since the process is exaggerated, because a possible method of locomotion is suggested which normally cannot be seen. Culture 5 contained a large frustule 575 μ long, 100 μ wide at its thicker end, and 75 μ wide at its thinner end. As illustrated, this frustule (*B*) when observed at 10:20 AM lay some 2 mm removed from the hydranth (*A*) from which it budded, yet it was still connected by an extremely delicate, but nevertheless distinct, "mucus" tube whose diameter was approximately 50 μ. By 11:00 AM this frustule slowly changed from a horizontal to a vertical position, only to assume again a horizontal position with its smaller end pointing away from *B*. By 4:00 PM it had moved to point *C* some 825 μ from *B*. Here, as at *B*, it slowly righted itself, only to assume again a horizontal
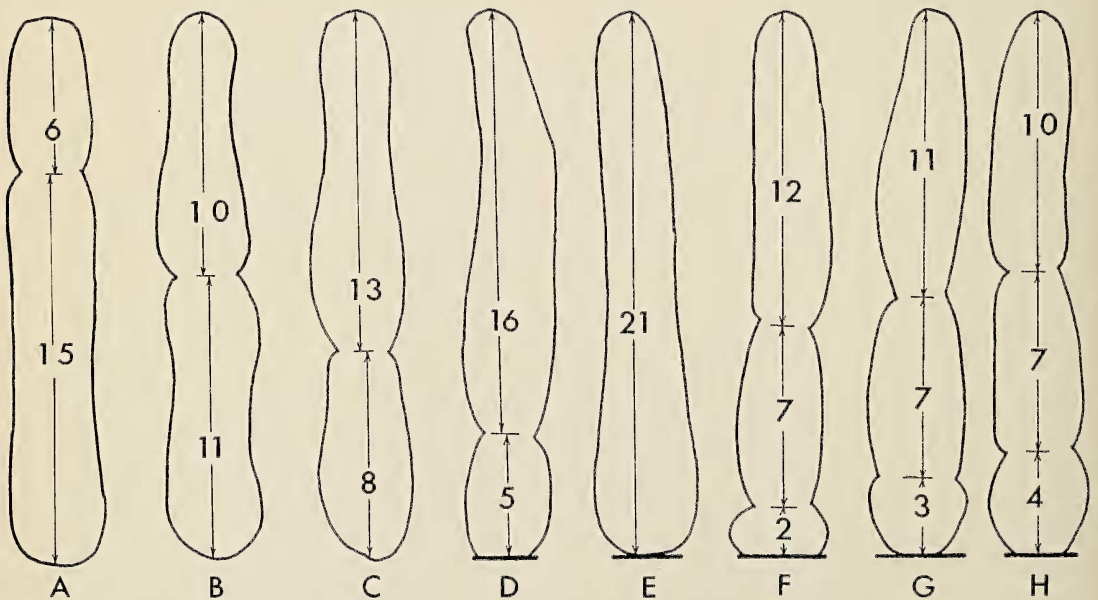

FIG. 10. Schematized drawing of frustules. *A, B, C,* and *D,* Changes in shape due to wave of contractility; *E,* failure of frustule to fragment; and *F, G,* and *H,* more than one wave operative. (Numbers correspond to ocular micrometer spaces of 25 μ and base line under *D, E, F, G,* and *H* signify attachment.)
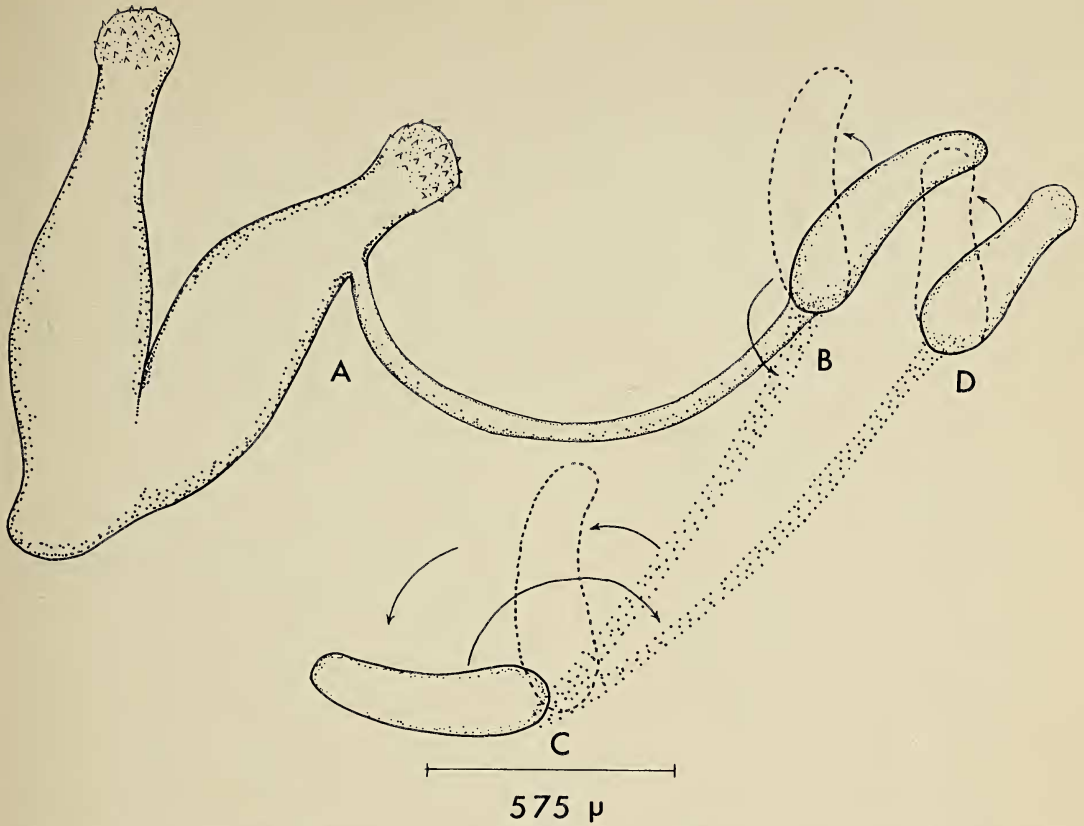
FIG. 11. Atentacular hydranth budding and frustule locomotion. *A,* Atentacular hydranth; *B,* frustule, horizontal (and *dotted,* vertical) at end of mucus tube; *C,* position of frustule at end of mucus carpet (*B–C*); and *D,* frustule attachment point at end of mucus carpet (*C–D*).

position with its smaller end pointing away from *C.* Next morning at 8:10 AM it had arrived at point *D,* about 850 μ from *C* and only about 175 μ from B. The thicker end was already attached, but the thinner end was elevated from the bottom of the Petri dish at about a 45° angle. It was no longer bean-shaped and was slowly metamorphosing into a young atentacular hydranth. It was now only 375 μ long and 125 μ wide at the thicker end; the thinner end still measured 75 μ wide. Next day, with the righting process completed, a capitulum developed. Exceedingly small, unidentified protozoa could be seen in the disintegrating tube between *A* and *B.* Regions between *B–C* and *C–D* lacked a lumen and thus were carpet-like. Toluidin blue (1:10,000) stained both tube and carpet very lightly, but in two days neither

was visible. Although this copious secretion was probably the result of Zn^{65} irritation, it is interesting that the frustule seemed to be more affected than the hydranth. The frustule's decrease in size and its abrupt, almost opposite change in direction support this view. Also, its change of position from horizontal to vertical and vice versa seems more related to mucus changes than to changes of buoyancy.

Frustules of untreated hydranths also remain attached for some time, but in no instance is their attachment so pronounced. In most instances, although the remaining connection could not be seen, its presence could be demonstrated by passing a small dissecting needle between hydranth and frustule.

During Part II of this study many stages were observed which at first sight strengthened the

contention that tentacular hydranths (Buchert's line V) metamorphosed into atentacular hydranths (Buchert's line II). Figure 12 is a diagram of a large tentacular hydranth which already has "absorbed" one row of its tentacles (which row would be pure speculation). Each tentacle is roughly 75 μ long and is further characterized by its swollen, almost spherical distal end. Because of the migration of nematocysts, these tentacles are extremely hyaline except distally, where three or four nematocysts often re-

main. Figure 12B is a diagram of the tentacular portion of another hydranth in which only 2 tentacles in the bottom row and 6 tentacles in the top row remain. Figure 12C is a diagram of a hydranth in which 10 stublike tentacles remain, but it is difficult to determine which stub belongs to which row. All are completely devoid of nematocysts. In Figure 12D only 5 stubby tentacles remain and, again, all are perfectly clear.

In these and other examples hydranths, teeming with bacteria and protozoa, became milk-colored and in a few days disintegrated. Not once did loss of tentacles result in development of atentacular hydranths.

Since neither (1) the ability of frustules or of frustule fragments of atentacular hydranths to produce tentacular hydranths nor (2) the ability of tentacular hydranths to metamorphose into atentacular hydranths can be demonstrated, the one-species concept lacks cogency.

III. *Calpasoma Dactyloptera* IN HAWAII

To my knowledge, this species has been reported only by Fuhrmann (1939, Switzerland), Buchert (1960, Hungary), Lytle (1960, Indiana, USA), and Rohat (1961, Israel), but because it is associated with *C. sowerbyi* it probably will be found to be quite common.

For the most part, Fuhrmann's original description (1939:365) fits well the Hawaiian representatives of this species. The general body size and shape, and the arrangement of the two rows of tentacles follow Fuhrmann's description as do the number, size (8–9 μ), and arrangement of nematocysts.

In all likelihood Fuhrmann had not made a study of the life cycle, which probably accounts for his statement, "We have seen only isolated individuals. The polyp does not appear to reproduce by budding, but mainly by transverse division. In fact, we have seen several polyps which show a constriction in the middle of the body which appears to be the start of this phenomenon" [author's translation]. It is also unfortunate that Buchert, who studied the life cycle and observed the budding of spherules, frustules, and hydranths, failed to place these in the correct species, because of lack of isolation of cultures.
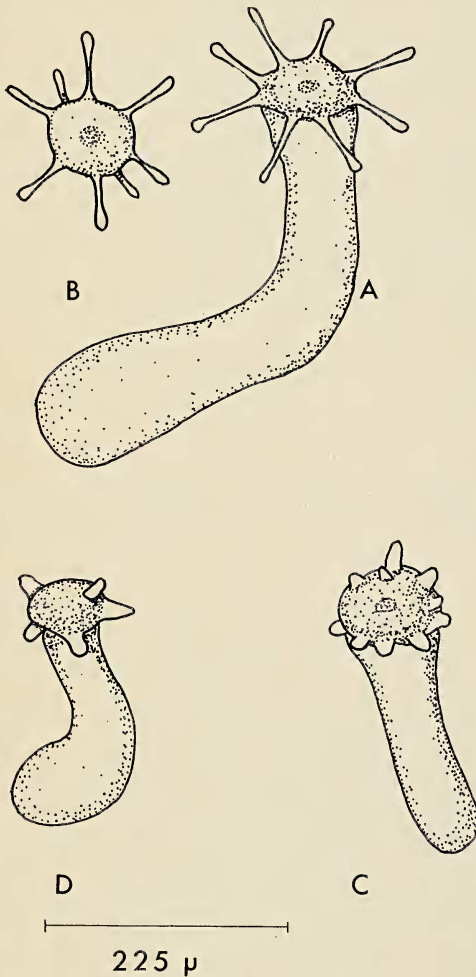

FIG. 12. Degeneration of tentacular hydranths. *A,* A large hydranth with but one row of tentacles; *B,* diagram of tentacular portion of hydranth with only two tentacles remaining in bottom row and six in top row; *C,* tentacular hydranth with only stublike tentacles remaining; and *D,* tentacular hydranth with only five, empty tentacle stubs remaining.
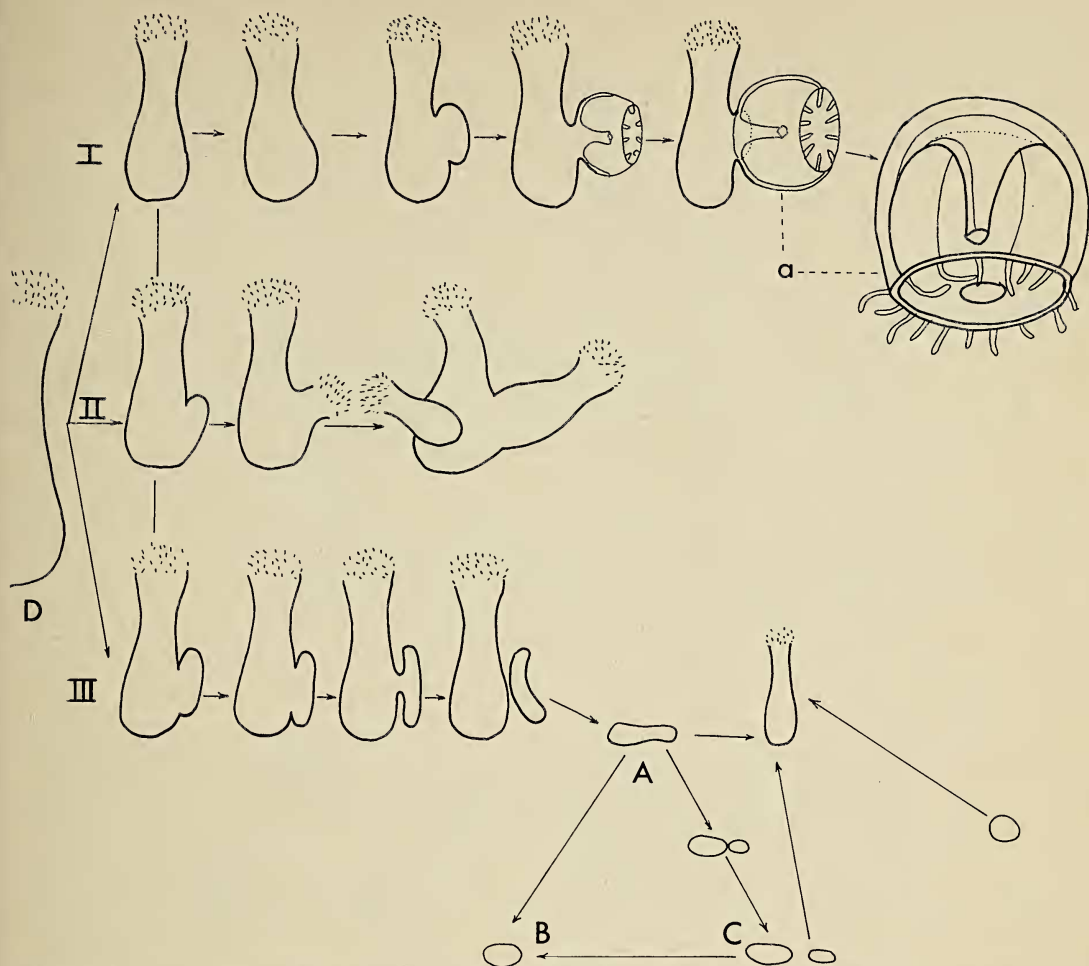
FIG. 13. Reproduction of Buchert's figures. Row *I*, medusa bud (*a*) formation; Row *II*, atentacular hydranth budding; and Row *III*, frustule budding. *A–B* and *C–B* indicate pathways by which tentacular hydranths are formed.

The study is by no means completed. As early as 1939, Fuhrmann (1939:368) said, "It is very probable that, under favorable conditions, the polyp forms a medusa like *Craspedacusta.*" In light of the variability of published photographs and drawings of *Craspedacusta* medusae, this suggestion has real merit.

Likewise, there is need for up-to-date, electron microscope studies of chromosome numbers in frustules. Although White (1930:230) states: "There seem to be twelve chromosomes at each pole of late anaphase of the primary spermatocyte," this number could not be verified in frustules since aceto orcein- and Feulgen-stained squashes (the latter, colchicine-pretreated) failed to reveal mitotic figures. The removal of cytoplasmic RNA by ribonuclease is now being atttempted, in the hope that only the DNA of the nucleus will take up the stain.
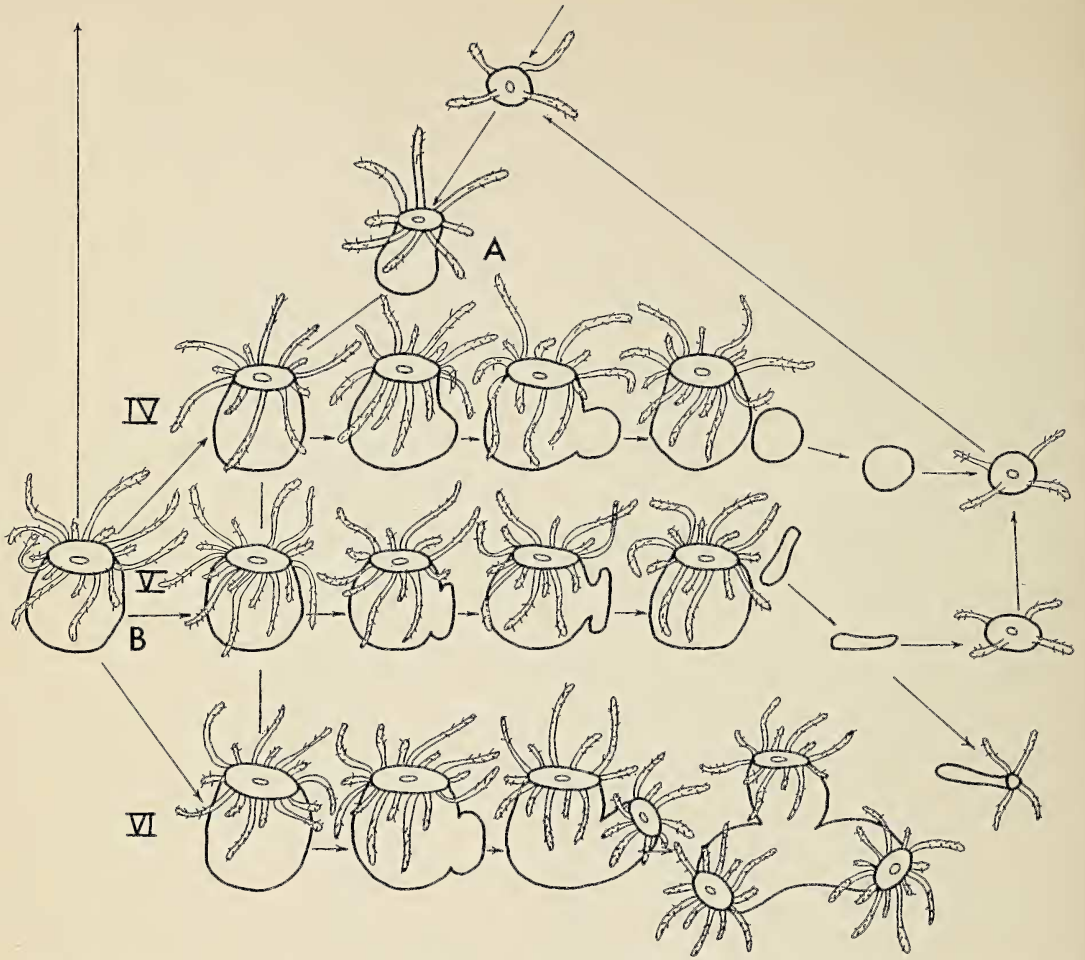
FIG. 14. Reproduction of Buchert's figures. Row *IV*, production of tentacular hydranths from spherules; Row *V*, frustule budding and formation of tentacular hydranths; and Row *VI*, tentacular hydranth budding. *A* indicates tentacular hydranth connecting atentacular and tentacular stages, and *B* indicates tentacular hydranth connecting atentacular stages (Fig. 13*D*).

whose generous hospitality enabled certain of us attending the XVI International Congress of Zoology to meet and to discuss *Craspedacusta*. I wish to credit Dr. Yanagita for improving the reliability of my nematocyst measurements. Above all others, I wish to thank Dr. C. F. Lytle who, although about to publish an account of tentacular hydranths which appeared in his culture of *C. sowerbyi* while he was at Indiana University, graciously forwarded copies of the papers by Buchert (1960), Fuhrmann (1939), and Rohat (1961).

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